# *Procymbulia philiporum* New Species, with a Discussion of the Genus *Procymbulia* Meisenheimer, 1905 (Gastropoda: Thecosomata)

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## ABSTRACT

*Procymbulia philiporum*, new species, is described from submersible collections in the Bahamas. This species retains a coiled shell but exhibits unique characters not known for other pseudothecosomes. It displays an extensive wingplate reminiscent of the family Cymbuliidae and encases its calcareous shell in a voluminous pseudoconch. Thus *P. philiporum* displays key characters of both the Peraclididae and the Cymbuliidae. This species is most appropriately placed in the genus *Procymbulia* Meisenheimer, 1905, within the Family Peraclididae Tesch, 1913, to distinguish its transitional nature.

*Key words:* Pteropod; Thecosomata; *Procymbulia*; *Peraclis*.

## INTRODUCTION

The genus *Procymbulia* Meisenheimer, 1905, was established from observations of a single preserved specimen of the type species, *P. valdiviae* Meisenheimer, 1905, collected in the southern Indian Ocean. This genus is of special interest since even the damaged specimens thus far described display various morphological characters that relate it both to the shelled *Peraclis* Forbes, 1844, and to the shell-less cymbuliids. Thus it has been considered a "missing link" (Meisenheimer, 1905; Tesch, 1913) between the shell-bearing genera of the Thecosomata and genera of the gelatinous pseudothecosomes (Cymbuliidae) which only possess a calcareous shell as larvae (*e.g.*, Lalli and Gilmer, 1989). Approximately 64 specimens from various expeditions and usually from deep tows have been ascribed to this genus (Bonnevie, 1913; Massy, 1932; Tesch, 1913, 1946, 1948; Hubendick, 1951). No species of *Procymbulia* has ever been collected intact. Tesch (1948) obtained sufficient shell remnants from the Dana Expedition material to piece together the shape of what he considered to be the shell of *P. valdiviae* Meisenheimer, 1905. Although the shell differed from those of all previously described *Peraclis* species, Tesch concluded that the morphological differences displayed by his specimens did not warrant the erection of a separate transitional genus.

I here describe the first living, intact specimen of a *Procymbulia* species, which I ascribe to a new species. It was collected alive at 902 m with a manned submersible. The animal exhibits key characters of both the Cymbuliidae and of the Peraclididae. These data warrant the reinstatement of the genus *Procymbulia* Meisenheimer, 1905.

## MATERIALS AND METHODS

In the present description of the new *Procymbulia* species I have assumed that the shell and wingplate axes run anterior-posterior (table 1). This terminology was established by Lalli and Gilmer (1989) for correct orientation of the body of pseudothecosomes (Families: Peraclididae, Cymbuliidae) to the shell and pseudoconch. Live pseudothecosomes are normally oriented with their ventral surface facing up. The proboscis and mouth are situated directly over the apex of the shell (in *Peraclis*) or over the blunt enlarged end of the pseudoconch (in cymbuliids). The median lobe of the wingplate is situated on the margin opposite the proboscis and lies directly over (ventral to) the pallial cavity opening. Thus the axis of the wingplate runs anterior-posterior in relation to the shell. This orientation is displayed by all live pseudothecosomes (excluding *Desmopterus* Chun, 1889) and bears no resemblance to descriptions of preserved specimens of *Peraclis* or *Procymbulia* species (*e.g.*, Meisenheimer, 1906; Tesch, 1948; Spoel, 1976). Preserved specimens are usually contracted and have the mantle cavity displaced laterally, towards the left or "dorsal" side of the shell in a manner that can resemble live specimens of the Limacinidae (Euthecosomata). Thus coiled pseudothecosomes are often erroneously considered analogous with the Limacinidae in regard to their body and shell orientation because of these preservation artifacts.

The single specimen was collected by the JOHNSON SEA-LINK I submersible using a 7.5 liter acrylic sampler

Table 1. Terminology used for orientation of soft part morphology of *Procymbulia* by various authors compared to the present description.

| Soft part | Meisenheimer (1905) | Tesch (1948) | This paper |
|---|---|---|---|
| Wingplate axis | dorsoventral | dorsoventral | anterior-posterior |
| Median lobe of wingplate | ventral | ventral | anteroventral |
| Proboscis | dorsal | dorsal | posteroventral |
| Tentacles | dorsal | dorsal | posterior |
| Pallial cavity | ventral | dorsal | anteroventral |
| Gill | — | ventral to right | anterior on midline |
| Anus | right | left | anterior on right |

with lids at either end that move horizontally over the openings to assure gentle collection (Tietze and Clark, 1986). The sampler is sealed when closed so that there is no exchange of water during return to the surface. The specimen was immediately transferred to a 0.5 liter glass dish and maintained at 8 °C on board ship for observation and photography. Photographs were taken using a Zeiss Tessovar macrolens fitted with an Olympus OM-2 camera body and dark field illumination. All photographs were taken with Kodak K-25 color slide film or Panatomic-X black and white film. The specimen was preserved in a 2% final solution of unbuffered glutaraldehyde and transferred to 70% ethanol after two weeks. The specimens was not dissected and is deposited in the National Museum of Natural History, Smithsonian Institution (USNM 860550).

## SYSTEMATICS

Family: Peraclididae Tesch, 1913
Genus: *Procymbulia* Meisenheimer, 1905

The original characters of this genus based on Meisenheimer's original description of *P. valdiviae* include: a ventral (see table 1) mantle cavity that opens beneath the wingplate opposite the margin bearing the proboscis; a cymbuliid-like gelatinous wingplate with similar muscle pattern; a more elongated proboscis than *Peraclis*; sensory processes bordering the median lobe of the wingplate; no opereulum; shell unknown, but presumed to be depressed based on soft part morphology.

*Procymbulia philiporum* new species
(figures 1–12)

**Description:** Coiled pseudothecosome pteropod but closely resembling *Corolla* Dall, 1871, in general appearance. Wingplate gelatinous, oval, highly patterned with muscle, transparent at margins but becoming thick and light brown near the centerline. Calcareous shell with four whorls, thin, brown colored, sinistrally coiled. Shell depressed; spire and body whorl with prominent growth striae parallel to aperture; aperture broad and drawn out in an elongated manner without a sharply pointed rostrum; columellar lip reduced. Shell internal within a voluminous gelatinous pseudoconch. Pseudoconch oval, *Corolla*-like in shape and consistency, length 1.5 × width, with broadly oval opening coinciding with shell aperture. Proboscis extending at 90° angle to wingplate surface, with darkly pigmented ciliary tracks surrounding mouth. Two unsheathed, equal tentacles on posterior surface of proboscis. Wingplate with distinct median lobe on anterior margin; lateral sensory processes on either side of median lobe but not extending beyond wingplate margin. No operculum present.

**Type locality:** Approximately 3 km SW of Moore Island in the Northwest Providence Channel, Bahamas (26°14.76′N, 77°43.46′W). Depth of collection: 902 m in midwater; time: 2300 hrs; 3 Nov 1989; temperature at collection depth: 6.7 °C; surface temperature: 28.5 °C. One specimen.

**Etymology:** This species in named in honor of Dr. Philip Pugh, the scientific observer, and Mr. Philip Santos, the submersible pilot, who together collected the specimen.

**Dimensions alive:** Wingplate width: 20.2 mm; pseudoconch length: 11.3 mm; pseudoconch maximum width: 7.3 mm; shell height: 7.5 mm, maximum shell width: 4.5 mm. **Dimensions preserved:** Wingplate width: 11.2 mm (highly contracted).

**Remarks:** *Procymbulia philiporum* possesses a finely sculptured, calcareous, sinistrally coiled shell (figures 1–10). It is very fragile and of a uniform chestnut brown color (figures 1, 2), differing considerably in structure from that of *P. valdiviae* as described by Tesch (1948). The shell of *P. philiporum* is distinguished by its well-defined growth striae (figures 1–10) that lie parallel to the aperture on the spire and body whorl. The spire is depressed (figures 9, 10). There are no keels or ribs along the suture and there are no spiral ribs on the body whorl as Tesch (1948) described as the major character of the shell of *P. valdiviae*. The anterior margin of the aperture

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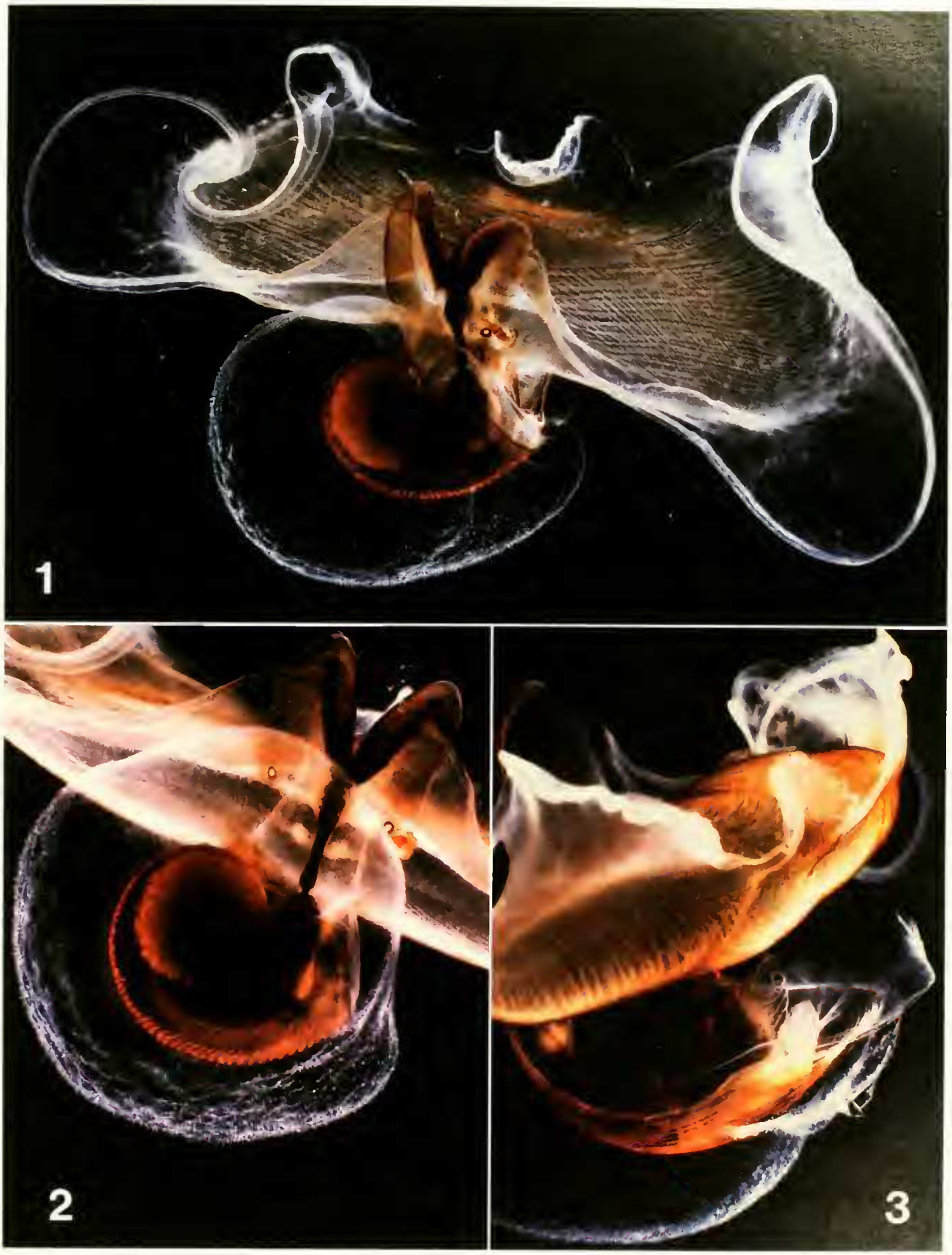
Figures 1–3. *Procymbulia philiporum* new species. **1.** From life, posterior view turned slightly so the left side and ventral surface of the wingplate are exposed. Compare with figure 4 for labels. Magnification ca. 8 ×. **2.** Posterior view, showing close up of shell apex and proboscis; compare with figure 7 for labels. Magnification ca. 12 ×. **3.** Anterior view from the left side showing exposed pallial cavity. The gill and pallial gland are visible; compare with figures 8 and 11 for labels. Magnification ca. 10 ×.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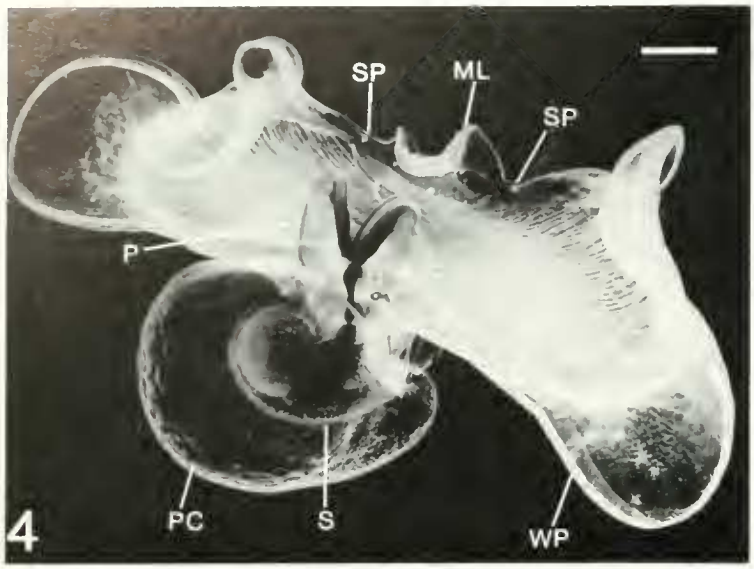
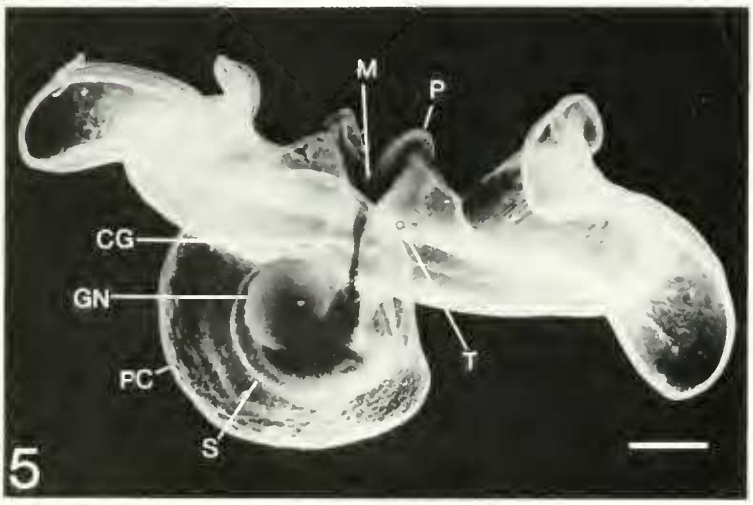
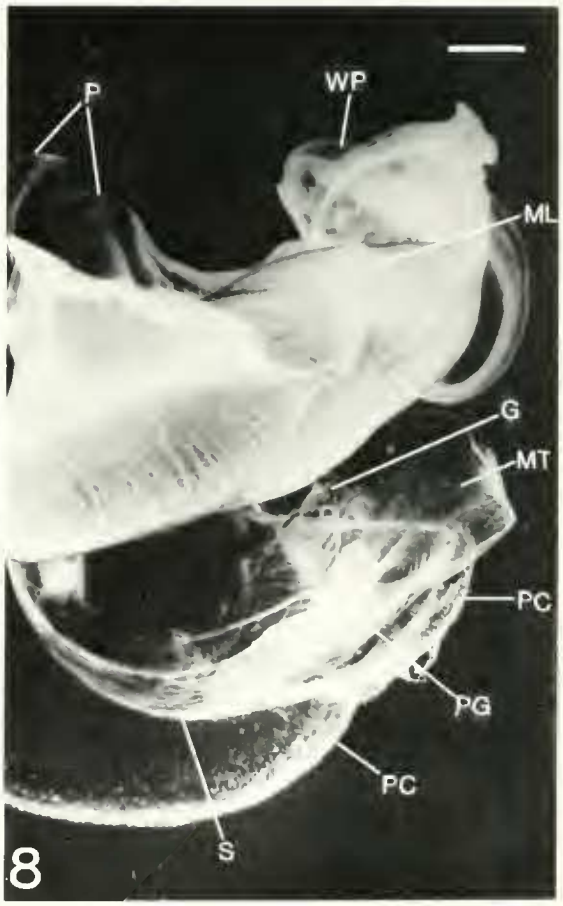
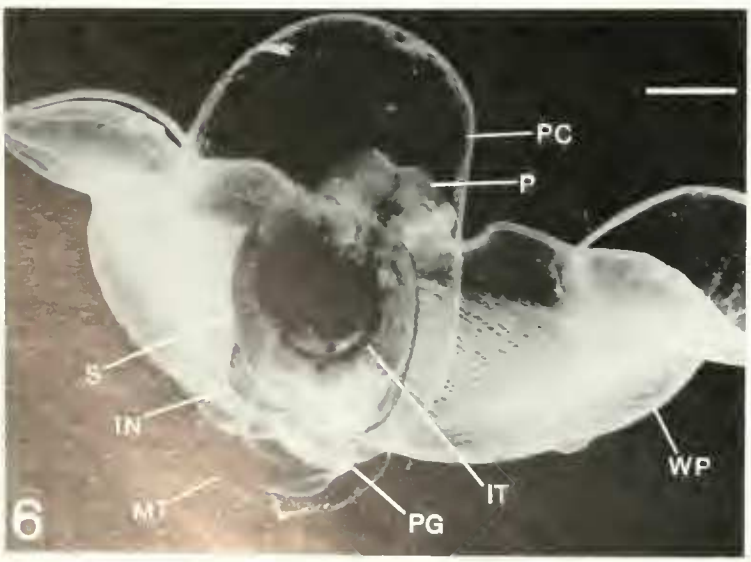






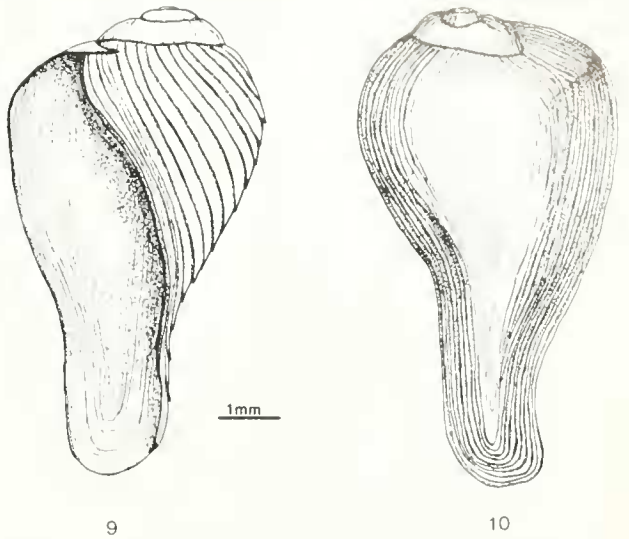

**Figures 4–8.** *Procumbrita pluliporum* new species. **4.** Posterior view showing the left and ventral surfaces, same as figure 1. Scale = 2 mm. **5.** Posterior view profile. Scale = 2 mm. **6.** Dorsal view; the proboscis is visible through the transparent pseudoconch. Scale = 2 mm. **7.** Posterior view showing close-up of shell apex and proboscis. Scale = 1 mm. **8.** Anterior view from the left side

(figure 9) is broadly expanded in an elongated manner without a sharply pointed rostrum, in contrast to the pointed rostrum of *P. valdiviae* (*i.e.*, Tesch, 1948) and of all *Peraclis* species. I detected no reticulation on the shell surface. The thin shell could not be removed from the animal without destruction. Consequently it dissolved after several weeks in the preservative.

The shell is enclosed in a large gelatinous pseudoconch (figures 1–8) of the same character and proportional size as those of cymbuliids. The pseudoconch is enclosed within a delicate layer of epithelium that does not appear to bear pigment or chromatophores as is common in the cymbuliids (Lalli and Gilmer, 1989). The pseudoconch appers to be connected to the shell surface by a series of fine threads (figure 7, FT). On the anterior end, there is a pronounced cavity between the shell and pseudoconch (figures 3, 8) that is lined with a dark brown layer of tissue. The pseudoconch also dissolved in the preservative although the epithelial layer that enclosed it remained as a membrane around the visceral nucleus.

The midline of the wingplate is situated directly over the posterior-anterior axis of the shell and pseudoconch (figures 1–7). The proboscis bearing the mouth (figures 4, 5, P) projects ventral-most at 90° from the posterior wingplate margin, directly over the apex of the shell and the blunt, posterior end of the pseudoconch. The expansive wingplate extends laterally and anteriorly, with a large median lobe (figures 4, 7, 8, ML) extending anterior-most, beyond the apertures of both the shell and pseudoconch. On either side of the median lobe, small dense patches occur near the wing border (figures 4, 11, SP) that appear to be concentrations of nerve fibrils and canals that converge from within the wingplate. They are not large, distinct processes as described in *P. valdiviae* (*cf.* Meisenheimer, 1905; Massy, 1932).

The wingplate is thick and heavily cross-patterned with muscle fibers (figures 1–8) which resemble the pattern seen in *Corolla* species (personal observation). The wingplate varies from almost transparent at the margins to light brown near the center line and around the base of the proboscis (figures 2, 7). The ciliated grooves of the lateral foot lobes nearest the mouth are nearly black in color (figures 2, 7), but become almost transparent at their distal margins (figure 1). The unpaired median foot lobe (figure 11, MFL) forms a low border anterior to the mouth and appears as a light brown extension off the wingplate. The paired tentacles (figure 5, T) resemble those of *P. valdiviae* (*cf.* Meisenheimer, 1905). They are of equal size, unsheathed, and lie on the posterior surface of the proboscis. The base of each tentacle is darkly pigmented but each terminates in a round, light-colored patch on the tip (figures 2, 7). The penis extends from




**Figures 9–10.** *Procymbulia philiporum* new species. **9.** Shell, ventral view showing aperture. **10.** Shell, dorsal view

an opening near the base of the proboscis, below (dorsal to) the left tentacle (figure 7, PN).

The pallial cavity opens broadly across the anterior portion of the shell aperture (figures 3, 8, 11). The anterior end of the pseudoconch is supported by a thick integument (figures 6, 11, IN) that extends from the pallial cavity. This integument appears to be the base of the epithelium that encloses the pseudoconch. Above (ventral to) this integument, a thick layer of the mantle (figures 6, 8, 11, MT) protrudes anteriorly beyond the aperture. The oval-shaped pallial gland is located on the ventral surface of this mantle layer. No "balancer" structure (*cf.* Meisenheimer, 1905) occurs on the mantle border of *P. philiporum*. Ventral to the pallial gland, a large plicate gill (figures 3, 8, 11, 12, G) originates from the right side of the visceral mass and extends anteriorly. When fully expanded in life, the gill protrudes slightly beyond the shell and lies along the midline of the pallial cavity, obscuring the pallial gland. The gill presents a large smooth surface with no deep furrows.

The intestine originates posteriorly, near the gonad (figure 12) and ends anteriorly on the right side of the pallial cavity near the gill. In its course (figure 12), it first encircles the viscera between the gonad and the digestive gland; it next extends anteriorly along the right side of the mantle cavity; it again encircles the anterior portion of the viscera before extending into the pallial cavity. The anus opens to the right of the gill at the end of a long and seemingly unsupported extension of the intestine (figures 11, 12, A). Because the anus and lower

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showing exposed pallial cavity with gill and pallial gland. Scale = 1 mm. Abbreviations: CG, central ganglion; FT, fine threads connecting shell and pseudoconch; G, gill; GN, gonad; IN, integument supporting anterior end of pseudoconch; IT, intestine; M, mouth; ML, median lobe of wingplate; MT, mantle tissue; P, proboscis; PC, pseudoconch; PG, pallial gland; PN, penis. S, shell; SP, sensory processes; T, tentacle; WP, wingplate.

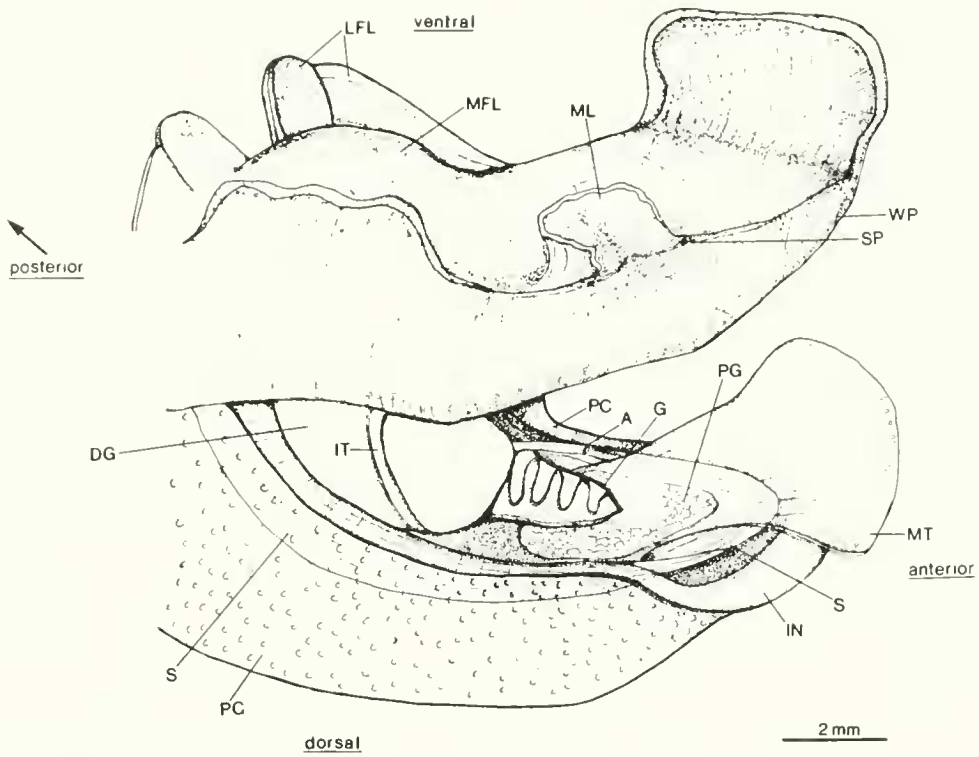


**Figure 11.** *Procymbulia philiporum* new species. Anterior view from the left side showing pallial cavity. Compare with figures 3 and 8. The posterior-anterior and dorsal-ventral axes of the shell are shown. The gill is retracted, but can extend beyond the anterior shell border. A, anus; DG, digestive gland; G, gill; IN, integument supporting pseudoconch; IT, intestine; LFL, lateral foot lobes (paired); MFL, median foot lobe (unpaired); ML, median lobe of wingplate; MT, mantle tissue; PC, pseudoconch; PG, pallial gland; S, shell; SP, sensory processes; WP, wingplate.

intestine have twisted back in a loop to the left side of the mantle cavity in the preserved specimen, the intestinal path of *P. philiporum* resembles the "Type A" diagram of Tesch (1948: figure 34E).

**Live observations:** The animal was neutrally buoyant in the center of the sampler on return to the surface and slowly swam about the container when disturbed. It swam by undulations of the wingplate in the manner of the cymbuliids (Morton, 1964; Lalli and Gilmer, 1989) and appeared to be healthy with no apparent signs of damage. The animal never attempted to retract into the shell even after severe prodding and indeed this would not appear possible given the size of the wingplate.

The intestine appeared to be full throughout its length, and several fecal pellets were produced during observation. The pellets were released into the pallial cavity and discarded off the anterior surface of the body by ciliary currents on the mantle. They were roughly 3 to 4 mm long and 0.5 mm in width. Recognizable contents included broken foraminifera tests, crustacean exoskeleton fragments, and coccolithophores. No particles in the fecal contents were larger than 40 $\mu$m.

## DISCUSSION

*Procymbulia philiporum* clearly displays characters of both the Peraclididae and the Cymbuliidae (Table 2), and points to the close affinity between these families. It therefore seems reasonable to reinstate the genus *Procymbulia* Meisenheimer, 1905, to emphasize its transitional nature. *Procymbulia philiporum* clearly shows close affinity to the family Peraclididae with respect to the coiled shell and the orientation of its internal organs. However, several new traits of the Peraclididae are now apparent based on this description: First, the shell can be totally enclosed in a gelatinous pseudoconch, similar to those characteristic of the Cymbuliidae. Secondly, the wingplate can have a broad highly gelatinous nature also similar to the Cymbuliidae. Thirdly, an operculum can be absent and the shell can lack suture ornamentation and a pointed rostrum. Lastly, the animal may not be capable of retraction into the shell.

Meisenheimer (1905) established *Procymbulia* as a transition genus mostly because the pallial cavity of his specimen was comparable in position to that of the cymbuliids and opposed by 180° in comparison to those of either *Peraclis* or *Limacina*. In fact, the pallial cavity and wingplate of living specimens of *Peraclis* species and *P. philiporum* have a similar orientation with respect to their shells and neither resembles the orientation of *Limacina*. More accurate characters on which to distinguish *Procymbulia* are the combined presence of the shell and pseudoconch, and the gelatinous *Corolla*-like wingplate.

Although *Peraclis* and *Procymbulia* have coiled shells, both display an important pseudothecosome trait by

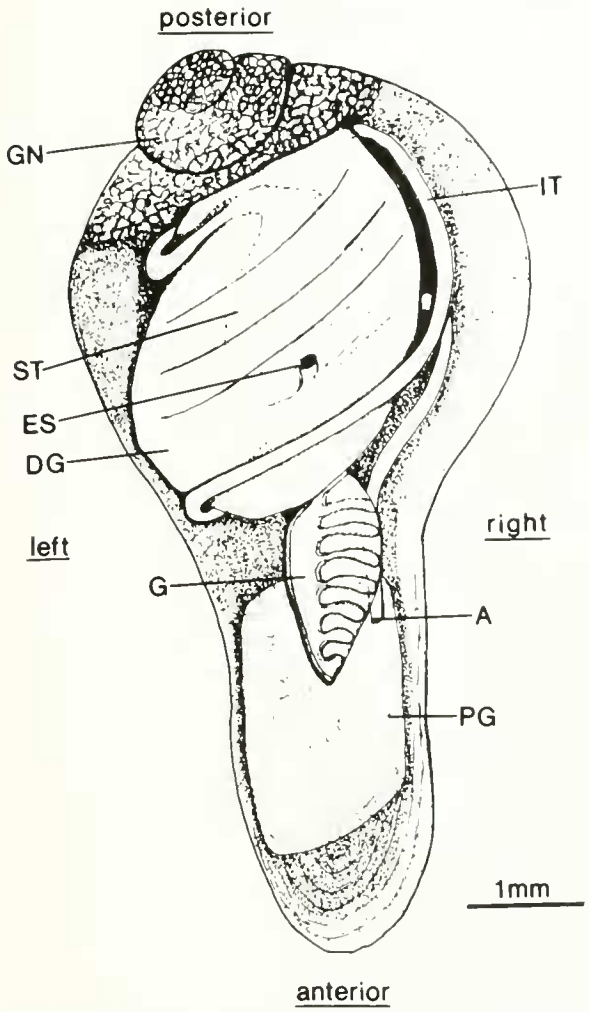


**Figure 12.** *Procymbulia philiporum* new species. Course of intestine (IT), mantle removed. A, anus; DG, digestive gland, ES, esophagus; G, gill; GN, gonad, PG, pallial gland; ST, stomach.

making them functionally internal structures (Gilmer and Harbison, 1986; personal observation). At least three species of *Peraclis* [*P. reticulata* (D'Orbigny, 1836), *P. bispinosa* Pelseneer, 1888 (figure 13), and *P. apicifulva* Meisenheimer, 1906] have mantle tissue that completely


**Figure 13.** *Peraclis bispinosa* from life, posteroventral view, wingplate (WP) fully expanded; mantle covering the shell (MT) is retracted so that the apex is visible. Scale = 2 mm. ML, median lobe of wingplate; P, proboscis; S, shell.

encloses the shell in life (personal observation). *Procymbulia philiporum*, however, more closely resembles the cymbuliids by encasing its shell in a pseudoconch, and by its apparent inability to retract into its shell possibly explaining the loss of the operculum. The wingplate of *P. philiporum* is also much more cymbuliid-like in thickness, muscle pattern, and general shape than I have seen in *Peraclis*.

Since Tesch (1948) closely linked *Procymbulia valdiviae* to *Peraclis bispinosa*, I have shown a partially expanded, living specimen of the latter species (figure 13) for comparison with *P. philiporum*. *Procymbulia bispinosa* has a more heavily pigmented wingplate and proboscis than *P. philiporum*, but the wingplate is reduced in thickness, in extent of muscle bands, and in size relative to the shell. The proboscis and gill[1] of *P. bispi-*

[1] Note: In a previous description of *Peraclis* (Lalli and Gilmer, 1989), we erred in stating that the gill was only retracted mantle tissue. I have now examined the gill in *P. reticulata*, *P. bispinosa*, and *P. apicifulva*.

**Table 2.** Comparison of major traits of the Peraclididae and Cymbuliidae prior to this description of *Procymbulia*.

| Peraclididae | Cymbuliidae |
|---|---|
| Coiled shell present with prolongation of columella | Calcareous shell in larval stage only |
| Shell axis oriented along posterior-anterior body axis | Body highly gelatinous, wingplate up to 2× body length |
| Shell often enclosed by voluminous mantle tissue | Shell replaced in adults by gelatinous pseudoconch |
| Operculum circular, glassy, left handed | Operculum left handed in larval forms |
| Proboscis comprised of three footlobes fused to wingplate | Proboscis similar, capable of great expansion in some genera |
| Anus opens to the right inside pallial cavity | Anus opens to left side of pallial cavity |
| Uniform pallial gland, without transparent bands | Pallial gland usually divided by transparent bands |
| Plicate ctenidium present in pallial cavity | No true ctenidium present |
| Well developed buccal mass present | Buccal mass reduced or absent in most species |
| Retracts completely into shell | No retraction mechanism after larval stage |

*nosa* are remarkably similar in structure to those of *P. philiporum*. Although *P. bispinosa* has extensive mantle that normally surrounds the shell, the live specimen in figure 13 was also carefully collected with the JOHNSON SEA-LINK and shows no evidence of a pseudoconch. In addition, *P. bispinosa* is capable of complete retraction into its shell.

Most descriptions of pseudothecosomes are greatly hampered by the condition of the material. Much of the described variation in *Peraclis* species is due to twisting of the pallial cavity or wingplate (*e.g.*, Tesch, 1948: figure 34a,b), during retraction. The mantle is much more extensive in living specimens than in preserved material which always shows tremendous variation. In addition, the same confusion in *Peraclis* regarding terms used to describe the orientation of the soft parts with the shell (Gilmer and Harbison, 1986; Lalli and Gilmer, 1989) also exists for *Procymbulia* (table 1).

Descriptions of *Procymbulia valdiviae* (Meisenheimer, 1905; Hubendick, 1951) suggest that the body and shell have an orientation similar to those of *P. philiporum*. Whether a pseudoconch is present remains unknown, although Massy (1932) described a firm membrane surrounding the viscera in her specimens. This tissue could be the epithelium that encloses the pseudoconch. It seems doubtful that the shell or pseudoconch of *P. philiporum* would ever survive the rigors of net collection or routine fixation. Both structures on my specimen dissolved within two weeks of preservation. A similar condition could be expected for *P. valdiviae*.

Tesch (1948) provided the most complete description of what he considered to be *Procymbulia valdiviae*. He found it so similar to *Peraclis bispinosa* that he removed its standing as a genus and discounted any transitional status it displayed between the Peraclididae and the Cymbuliidae. However, five facts suggest that the specimens Tesch used to make his determination are probably a new species of *Peraclis* rather than specimens of *P. valdiviae*: 1) the shells bear distinct *Peraclis*-like rostra and suture ornamentation; 2) the shells survived net collection and years of preservation; 3) only his specimens bear an operculum; 4) Tesch's figures show a *Peraclis*-like 90° twisting of the wingplate, indicating partial retraction into the shell. Figures of *P. valdiviae* from Meisenheimer (1905), Bonnevie (1913), Hubendick (1951), and my preserved specimen of *P. philiporum* all have the wingplate situated in its unretracted position (the proboscis over the gonadal whorl) suggesting *Procymbulia* does not display this type of retraction. And finally, 5) Tesch found no lateral processes bordering the median lobe of the wingplate.

*Procymbulia* appears to be cosmopolitan in its distribution and represented by at least two species. Based on the collections of Meisenheimer (1905) and Massy (1932), it would appear that *P. valdiviae* probably occurs in the circumglobal southern oceans, primarily in deep water. As stated above, Tesch's (1948) Indo-Pacific specimens most likely belong to a new species of *Peraclis*. Bonnevie's (1913) description of *P. michaelsarsi* from a single specimen collected in the N.E. Atlantic may be very similar to *P. philiporum*. Based on her brief description, the shape of the gonadal whorl and the orientation and pigmentation pattern of the proboscis resemble *P. philiporum*. Hubendick (1951) and Tesch (1946) may also have collected *P. philiporum*, since all of these Atlantic specimens assigned to *P. valdiviae* lack the large sensory processes on the anterior wingplate margin characteristic of this latter species. Hubendick's figures closely resemble my preserved specimen, and Tesch (1946) described a similar pigment pattern to that of *P. philiporum* but indicated that an operculum was attached to the wingplate of his specimens. My animal shows no scar or other indication of ever having had an operculum. Tesch's specimens were considerably smaller than mine, however, and the operculum may be lost at an early age.

## ACKNOWLEDGEMENTS

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## LITERATURE CITED

Bonnevie, K. 1913. Pteropoda. Report of the "Michael Sars" North Atlantic Deep Sea Expedition 3:1–85.

Gilmer, R. W. and G. R. Harbison. 1986. Morphology and field behavior of pteropod molluscs: feeding methods in the families Cavoliniidae, Limacinidae and Peraclididae (Gastropoda: Thecosomata). Marine Biology 91:47–57.

Hubendick, B. 1951. Pteropoda, with a new genus. Further Zoological Results of the Swedish Antarctic Expedition 1901–1903 4(6):1–10

Lalli, C. M. and R. W. Gilmer. 1989. Pelagic snails. The biology of holoplanktonic gastropod mollusks. Stanford University Press, 259 p.

Massy, A. L. 1932. Mollusca: Gastropoda Thecosomata and Gymnosomata. Discovery Reports 3:267–296.

Meisenheimer, J. 1905. Pteropoda. Wissenschaftliche ergebnisse der Deutschen Tiefsee Expedition auf dem Dampfer "Valdivia" 1898–1899 9(1):1–314

Meisenheimer, J. 1906. Die Pteropoden der deutschen Südpolar-Expedition 1901–1903. Deutsche Südpolar-Expedition IX Zoologie 1:94–153.

Morton, J. E. 1964. Locomotion. *In:* Wilbur, K. and C. M. Yonge (eds.). Physiology of the Mollusca. Academic Press, 1:383–423.

Spoel, S. van der. 1976. Pseudothecosomata, Gymnosomata

and Heteropoda (Gastropoda). Bohn, Scheltema, and Holkema, Utrecht, 484 p.

Tesch, J. J. 1913. Pteropoda. *In:* F. E. Schulze (ed.). Das Tierreich. R. Friedländer & Sohn, Berlin, 36:1–154.

Tesch, J. J. 1946. The thecosomatous pteropods. I The Atlantic. Dana Reports 28:1–82.

Tesch, J. J. 1948. The thecosomatous pteropods II The Indo-Pacific. Dana Reports 30:1–45.

Tietze, R. C. and A. M. Clark. 1986. Remotely operated tools for undersea vehicles. *In:* T. McGuiness (ed.). Current practices and new technology in ocean engineering. American Society of Mechanical Engineers 11:219–223.